Giving and receiving: the tropical Atlantic as donor and recipient region for invading species

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Abstract: After the middle Pliocene uplift of the Central American seaway (3.1 to 3.6 million years ago), the western Atlantic fauna became isolated from that of the eastern Pacific, but connections with the tropical Indo-West-Pacific and eastern Atlantic were maintained. By analyzing the distibution, fossil record, and relationships of shallow-water shell-bearing molluscs (those living in less than 100 m depth) in the western Atlantic, we ascertained the extent to which the western Atlantic has served as a recipient and as a donor region for invading taxa.

At least 33 species in the western Atlantic are late Pliocene or Pleistocene invaders from the Indo-West-Pacific (17 species) or eastern Atlantic (16 species), whereas at least 39 species dispersed eastward across the Atlantic from the Americas to West Africa. Eleven species derived from the Indo-West-Pacific are included in both tallies, because they probably first dispersed westward from the Indian Ocean around southern Africa to Brazil and the Caribbean region before spreading eastward across the Atlantic to West Africa. Most of this dispersal is probably by means of planktonic larvae, but some species could have been spread as rafting adults.

Oceanic currents and prior extinction histories determine the pattern of interchange among tropical marine biotas. Within the tropics, the western Atlantic suffered the greatest molluscan extinctions since the early Pliocene (about 60 to 70%); it is also the region in which the great majority of immigrants have become common and geographically widespread. Extinction in the eastern Atlantic, eastern Pacific, and Indo-West-Pacific has been much less, and immigrants to these regions often have restricted geographical distribution there, and could be represented by populations that are not self-sustaining.

Biogeographers working with living species have divided the biosphere into a number of provinces, each of which is characterized by species found only in that region. The often unstated assumption is that these provinces have a certain continuity and cohesiveness, and that therefore they can be treated as biologically meaningful units above the species level. A consequence of this interpretation is that biogeography has been pervaded by attempts to define boundaries between provinces and to establish criteria for recognizing a region as biogeographically distinct.

As we learn more about the phylogenetic relationships and fossil record of species, the idea of provincial purity and integrity is giving way to the realization that many geographical regions support species whose geographical origins and histories vary widely. Some evolved in the region they presently occupy, whereas others arose or evolved elsewhere. There is abundant evidence that the distributional limits of species change over the course of time. For example, if a species is initiated as a small geographical isolate, it often expands its range subsequently. Other species undergo range contractions as local populations become extinct. These considerations lead to a more dynamic view of provinces, one that admits extinctions and invasions of species. Changes in the distributional limits of species affect the distinctiveness as well as the boundaries of provinces. Instead of ascertaining where these boundaries should be drawn, we can ask to what extent regions have served as sources for invading species, as refuges for species that have contracted their ranges, and as places suitable for the successful establishment of species that originated elsewhere.

Answers to these questions require a fossil record that is biogeographically and statigraphically sufficient to trace the histories of many lineages. The Neogene record of shell-bearing molluscs, though necessarily incomplete and insufficiently known in some regions, is, nonetheless, ideal for this purpose. Coupled with cladistic and molecular studies, analyses of this record could reveal much about the dynamics of species distributions and about the integrity of biogeographical provinces.

In this paper we devote particular attention to biogeographical connections between the tropical western Atlantic and other tropical marine regions. Before mid-Pliocene time (about 3.1 to 3.6 million years ago), the Central American seaway connected the western Atlantic with the eastern Pacific, so that many species were held in common between these two regions. The connection was interrupted by the mid-Pliocene uplift of the Central American isthmus. Connections between the western Atlantic and the two other tropical marine regions, the Indo-West-Pacific and eastern Atlantic, were maintained, however. Dispersal of planktotrophic larvae and rafted

adults westward or eastward across the Atlantic maintains a faunal connection between the eastern and western Atlantic (Scheltema, 1971). The link with the Indo-West-Pacific is by way of dispersal around South Africa from the southwestern Indian Ocean to the central and western Atlantic.

By analyzing the distribution, history, and relationships of western Atlantic shell-bearing molluscs, we ask two related questions in this paper. First, to what extent and by which molluscan lineages has the western Atlantic been invaded from elsewhere in the tropics during the last three million years? Second, to what extent has the western Atlantic contributed invaders to other tropical regions during the last three million years, and which lineages have taken part in this invasion?

METHODS

We have compiled data on the geographical distribution, fossil record, and relationships of shell-bearing molluscs living in the tropical western Atlantic, an area we define as extending from Cape Hatteras, North Carolina, USA, to the vicinity of Rio de Janeiro, Brazil. Our aim was to identify species that invaded either westward or eastward across the Atlantic following the mid-Pliocene uplift of the Central American isthmus. To that end, we compiled a list of all amphi-Atlantic species (those living on both sides of the Atlantic), based largely on the primary taxonomic and systematic literature. We have also relied heavily on the faunistic accounts of von Cosel (1982), for the Cape Verde Islands, and Leal (1991), on the fauna of islands and sea mounts off Brazil. Some of the purported cases of amphi-Atlantic distributions are not based on a critical comparison of eastern and western Atlantic specimens. Some of the cases we report could therefore turn out to represent pairs of closely related eastern and western Atlantic species. In his compilation of amphi-Atlantic species, Talavera (1982) included many species whose distribution on both sides of the Atlantic is clearly in error or not well documented. We have therefore chosen not to include Talavera's amphi-Atlantic records unless other sources corroborate such a distribution. Wood-boring pholadid and teredinid bivalves were also excluded.

Species were inferred to have invaded during the last three million years to the western Atlantic from elsewhere in the tropics if (1) they or their likely ancestors are unknown as fossils in the western Atlantic before mid-Pliocene time, (2) they or their ancestors have a fossil record earlier than Pliocene elsewhere in the tropics, and (3) they have no close relatives (ancestral or sister species) in the tropical eastern Pacific. The rationale for the first and second criteria is obvious, but the third criterion requires

brief explanation. If a western Atlantic species has a close fossil or living relative in the eastern Pacific, we can infer that the species or its ancestor was already present in tropical America during or before mid-Pliocene time, when the Central American seaway was still open. The vast majority of western Atlantic species with close eastern Pacific relatives indeed have fossil records extending to early Pliocene and often Miocene time.

We have excluded from this analysis all species that live only in waters more than 100 m deep. As a rule, deepwater taxa are not well represented in the fossil record, so that direct historical evidence from the fossil record is often lacking. Moreover, an amphi-Atlantic distribution could reflect a continuous benthic population of adults rather than a link between eastern and western populations maintained by overwater dispersal.

Potential invaders to the western Atlantic were divided into two groups. The first is composed of species that probably came from the Indo-West-Pacific around southern Africa at a time when the coastal waters of south Africa were warmer than today. Species belonging to groups with a long fossil record in the Indo-West-Pacific but not the eastern Atlantic were assigned to this group of invaders. The second group is composed of amphi-Atlantic species whose fossil record in the eastern Atlantic extends back beyond mid-Pliocene time. Amphi-Atlantic species found only on offshore islands in either the eastern Atlantic (Cape Verde and Canary Islands, for example) or the western Atlantic (Lesser Antilles or Fernando de Noronha, for example) were distinguished from those that occur on the coasts of the continents.

The western Atlantic could have contributed species to other tropical regions since the mid-Pliocene. Potential invaders from the western to the eastern Atlantic were identified in cases where the eastern Atlantic fossil record is no older than mid-Pliocene.

Many amphi-Atlantic species do not fall into either group of invaders. Some species will have achieved their amphi-Atlantic distribution before the mid-Pliocene. Others are not well understood taxonomically, biogeographically, or paleontologically. We have compiled a list of all shallow-water shell-bearing amphi-Atlantic species but we have not attempted to trace their history of invasion.

INVADERS FROM THE INDO-WEST-PACIFIC

At least 20 western Atlantic gastropods are inferred to have arrived from the Indo-West-Pacific region since mid-Pliocene time (Appendix 1). Of these, 11 species (indicated by an asterisk) are endemic to the Atlantic but have their closest relatives in the Indo-West-Pacific. For exam-

ple, the trochid *Synaptocochlea picta* of the western Atlantic is the only member of its genus in the Atlantic, and is very similar to *S. concinna* (Gould, 1845), known from the Pleistocene and Recent of the Indo-West-Pacific (see Kay and Johnson, 1987; Leal, 1991). The cassid *Casmaria atlantica* is the only Atlantic species of its genus. It is extremely similar to the Indo-West-Pacific *C. ponderosa* (Gmelin, 1791), especially to the Indian Ocean form sometimes given the name *C. cernica* (Sowerby, 1888) (see Abbott, 1968). The only eastern Pacific species of *Casmaria, C. vibexmexicanum* (Stearns, 1894), is in the *C. erinacea* (Linnaeus, 1758) species complex and is not close to either *C. atlantica* or *C. ponderosa* (Abbott, 1968). The genus *Casmaria* has a Pleistocene fossil record in the western Pacific and Indian Oceans but is not known as a fossil in the Atlantic. Gibson-Smith and Gibson-Smith (1981) tentatively suggested that *C. atlantica* arose via *Phalium (Tylocassis) cicatricosum* (Gmelin, 1791) from the New World *P. granulatum* line, which appeared during the early Miocene. They pointed to similarities in protoconch characters and in the lack of sculpture on the later teleoconch whorls. This scenario requires that the outer-lip prickles characteristic of *Casmaria* evolved independently in the Indo-West-Pacific member of this genus and in *C. atlantica*. We reject this scenario in favor of the simpler idea that *C. atlantica* is derived from an Indian Ocean form of *C. ponderosa*, which entered the Atlantic during relatively recent time. The tonnid *Eudolium crosseanum* of the Atlantic is close to the Indo-West-Pacific *E. pyriforme* Sowerby, 1914 (see Marshall, 1992). The genus *Eudolium* is known from the Oligocene onward in the eastern Atlantic and from the early and late Miocene of the eastern United States, but *E. crosseanum* and the Atlantic and Indo-West-Pacific *E. bairdii* may not have descended from these earlier forms and are themselves not known as Atlantic fossils. *Malea (Quimalea) noronhensis*, known only from islands off Brazil (Leal, 1991), is very similar to the widespread Indo-West-Pacific *Malea pyrum* (Linnaeus, 1758). It is the only New World representative of the subgenus *Quimalea*. All other fossil and living species of *Malea* in the Americas belong to the nominate subgenus (see Petuch, 1989). The genus *Tonna* is unknown as a fossil in the Americas. *T. galea* is known living in both the Atlantic and the Indo-West-Pacific region, but *T. maculosa* is endemic to the Atlantic, being closely similar to the Indo-West-Pacific *T. perdix* (Linnaeus, 1758). The ranellid *Cymatium (Septa) occidentale* is the only Atlantic representative of the *C. rubeculum* (Linnaeus, 1758) species complex of the Indo-West-Pacific (Beu, 1986). *C. (Ranularia) ridleyi* of the western Atlantic is very similar to *C. sarcostomum* (Reeve, 1844) from the Indo-West-Pacific. Among the Bursidae, the western Atlantic *Bursa natalensis* is very close to, and

sometimes synonymized with, *B. latitudo* Garrard, 1961 (for a discussion see Leal, 1991). *Bursa thomae* is extremely similar to the Indo-West-Pacific *B. rhodostoma* (Sowerby, 1871). A fossil possibly related to *B. thomae* was described by Jung (1969) from the Pliocene Melajo Clay of Trinidad. *Bufonaria (Marsupina) bufo* is the only member of its genus in the Atlantic; all other members are Indo-West-Pacific in distribution. Because *B. bufo* differs at the subgeneric level from other members of *Bufonaria*, the possibility exists that this species has been in the Atlantic since before mid-Pliocene time. However, it is unknown as a fossil and has no close relatives in the eastern Pacific fauna. Finally, the architectonicid *Psilaxis krebsii* of the Atlantic is extremely close to the Indo-West-Pacific *P. oxytropis* (A. Adams, 1855). It is known fossil from the late Pliocene or early Pleistocene Bowden Formation of Jamaica (as the subspecies *lampra* Woodring, 1928) and may therefore have arrived from the Indo-West-Pacific as early as the late Pliocene (see Robertson, 1973).

Besides *Bursa thomae* and *Psilaxis krebsii*, only one other species inferred to have arrived in the Atlantic from the Indo-West-Pacific after uplift of the Central American isthmus has a fossil record in the New World. Robinson (1990) reported *Gyrineum louisae* from the early Pleistocene Moín Formation of Costa Rica.

It is possible that several Atlantic taxa with eastern Pacific counterparts also arrived in the Atlantic directly from the Indo-West-Pacific, and that they are therefore not derived from ancestors living in the New World before the closure of the Central American isthmus. Examples include the ranellids *Cymatium aquatile, C. cynocephalum, C. labiosum, C. mundum, C. muricinum, C. nicobaricum, C. parthenopeum, Charonia tritonis variegata, Linaetella caudata* (see e.g. Beu and Cernohorsky, 1986; Beu and Knudsen, 1987; Beu and Kay, 1988). The eastern Pacific representatives probably arrived in the New World from the west after uplift of the isthmus, along with numerous other species, and independently of the invasion of the same stocks to the tropical Atlantic (see Emerson, 1991). Which scenario is correct cannot be resolved with the presently available evidence, but for now we have chosen to be conservative by not including the above species as immigrants to the Atlantic directly from the Indo-West-Pacific.

The inference of invasion from the Indo-West-Pacific to the Atlantic is based in part on negative evidence, namely, the absence of a pre-Isthmian New World fossil record. Such evidence is, of course, always suspect. It is always possible that some of these species were already present in the Atlantic at the same time the Central American seaway closed. This could apply to *Bursa (Lampadopsis) grayana* (Dunker, 1862) (= *B. pacamoni* Matthews and Coelho, 1971), a species today known only from Brazil.

This bursid is very close to *B. davidboschi* Beu, 1986, from the Indian Ocean, and could have been descended from an Indo-West-Pacific population. Beu (1986), however, has recorded *B. grayana* from the early Pliocene or late Miocene Gurabo Formation of the Dominican Republic. If the species did arrive from the Indo-West-Pacific region, it could have done so well before the isthmus in Central America was uplifted and without leaving eastern Pacific relatives. It is possible that other Atlantic species whose affinities lie with Indo-West-Pacific species will also be recovered as pre-isthmian fossils in the New World. In the absence of such evidence, however, and given that there are no close relatives in the eastern Pacific, we prefer the interpretation that these Atlantic species are post-isthmian invaders from the Indo-West-Pacific.

We have not included the ranellid *Linatella succincta* in the list of invaders to the Atlantic from the Indo-West-Pacific. The species is apparently unknown as a fossil, and is closely related or identical to forms from the eastern Pacific and Indo-West-Pacific (Emerson, 1991). Within the Atlantic, the species occurs on the African coast only in Gabon (Beu and Cernohorsky, 1986). It is possible that *L. succincta* is an invader from the Indo-West-Pacific, but the evidence in favor of this conclusion is not persuasive.

Of the 20 invaders from the Indo-West-Pacific to the Atlantic (Appendix 1), 11 (55%) occur on both sides of the Atlantic (Appendix 2). Six of these 11 species, however, have extremely limited distributions in the eastern Atlantic. *Bursa ranelloides, B. thomae, Cymatium occidentale,* and *Tonna maculosa* occur in the eastern Atlantic only on off-shore islands (Appendix 2), whereas *Eudolium bairdii* and *E. crosseanum* are known from only a few Mediterranean records (Marshall, 1992). This implies that these species or their ancestors came directly from the Indo-West-Pacific to the western Atlantic and subsequently dispersed to the eastern Atlantic. Further support for this interpretation comes from the fact that six of the Indo-West-Pacific immigrants or their descendants are known in the Atlantic only from the American side, and that no immigrants are limited in the Atlantic to the African side. We believe that that principal dispersal route was from the southwestern Indian Ocean around southern Africa to St. Helena and thence northward and westward to Brazil and the Caribbean Region. Such dispersal is likely only at times when southern Africa was warmer than it is today. St. Helena's marine fauna of molluscs and crustaceans is well known for the presence of taxa known otherwise only from southern Africa or the Indo-West-Pacific (E. A. Smith, 1890; Chace, 1966).

DISPERSAL ACROSS THE ATLANTIC

We recognize 123 shell-bearing molluscs as occur-ring in shallow waters (less than 100 m deep) on both sides of the tropical and subtropical Atlantic (Appendix 2). Of these, 108 are gastropods, 15 are bivalves, and one is a scaphopod. Eleven of the amphi-Atlantic species (all gastropods) are inferred to have arrived from the Indo-West-Pacific after the Central American seaway was closed; they were dealt with in the preceding section. Most of the remaining 113 amphi-Atlantic species or their ancestors already existed in the Atlantic basin when the Central American seaway was still open. Some of these species could already have had an amphi-Atlantic distribution at that time. At least 43 species (37 gastropods, 6 bivalves) are inferred here to have dispersed either eastward or westward across the Atlantic following the mid-Pliocene uplift of the Central American isthmus (Tables 1-3). Of these 44 species, 28 dispersed eastward from the Americas to the coasts of Europe and West Africa, whereas 15 dispersed westward. These numbers exclude the previously discussed immigrants from the Indo-West-Pacific, which are inferred to have dispersed first westward across the south Atlantic and then secondarily eastward again to the eastern Atlantic.

A majority (22 species, 79%) of the 28 taxa inferred to have dispersed eastward from the Americas to the African side of the Atlantic have very limited distributions in the eastern Atlantic. For example, the fissurellid keyhole limpet *Diodora cayenensis* is known in the eastern Atlantic only from the Canary Islands, whereas on the American side it is widespread (Leal, 1991). As a fossil, this species is known not only from the western Atlantic, but also from the eastern Pacific, where Schremp (1981) recorded it from the early Pliocene Imperial Formation of Southern California.

The small littorinid *Nodilittorina (Fossarilittorina) meleagris* is known in the eastern Atlantic only from Ghana (Rosewater and Vermeij, 1972; Rosewater, 1981), but in the western Atlantic it has a wide distribution. The species is unknown as a fossil, but all other species of the subgenus *Fossarilittorina* occur in the western Atlantic and eastern Pacific (Rosewater, 1981; Reid, 1989).

The calyptraeid *Crepidula (Bostrycapulus) aculeatus,* which is known in the eastern Atlantic only from the Cape Verde Islands (von Cosel, 1982), lives in both the western Atlantic and eastern Pacific. It has a fossil record in eastern North America extending back to the middle Miocene (Hoagland, 1977).

The helmet shell *Cassis tuberosa* (Cassidae) occurs in the Cape Verde Islands and nowhere else in the eastern Atlantic (von Cosel, 1982). The lineage of *C. tuberosa* was present during the early Miocene in Florida, and was represented in the eastern Pacific during the early Pliocene (Vokes, 1990). The cassid *Phalium (Tylocassis) granulatum* is also insular in the eastern Atlantic, but in the Americas

the subgenus *Tylocassis* occurs in the late Miocene Gatun Formation of Panama and is represented by living species in both the western Atlantic and eastern Pacific (Abbott, 1968). Exactly the same applies to the bursids *Bursa corrugata* and *B. granularis,* the buccinid *Colubraria testacea,* and the bivalves *Arca imbricata* (Arcidae), *Arcopsis adamsi* (Noetiidae), *Dendostrea frons* (Ostreidae), and *Pseudochama radians* (Chamidae) (see Woodring, 1964, 1973; Beu, 1980; von Cosel, 1982; Leal, 1991).

A number of amphi-Atlantic species confined in the eastern Atlantic to offshore islands perhaps also have dispersed eastward from the Americas, but the evidence from the fossil record and systematic relationships is weaker. Species in this category include the hipponicids *Hipponix antiquatus* and *H. subrufus,* the naticids *Natica livida* and *Polinices lacteus,* and the ranellids *Cymatium aquatile, C. labiosum,* and *C. muricinum.* Most of these species are closely related or identical to Indo-West-Pacific as well as to eastern Pacific species, so that we cannot be sure when or in what way they achieved an amphi-Atlantic distribution. We have included them among eastward dispersers (Table 1) because there is no fossil record of these species in the eastern Atlantic. In the case of *C. labiosum,* there are late Pliocene or early Pleistocene records in the western Atlantic from the Bowden Formation of Jamaica and the Móin Formation of Costa Rica (Beu and Knudsen, 1987). *C. aquatile* is known from the Pliocene of Ecuador in the eastern Pacific (Beu and Kay, 1988).

TABLE 1. Eastward-dispersing species in the tropical Atlantic.

Diodora cayenensis
Lucapinella limatula
Cheilea equestris
Crepidula aculeata
Hipponix antiquatus
H. subrufus
Nodilittorina meleagris
Natica livida
Polinices lacteus
Bursa corrugata
B. granularis
Cymatium aquatile
C. labiosum
C. muricinum
Linatella caudata
Cassis tuberosa
Phalium granulatum
Thaisella coronata
Trachypollia nodulosa
T. turricula
Colubraria testacea
Coralliophila caribaea
Arca imbricata
Arcopsis adamsi
Nodipecten nodosus
Dendostrea frons
Pseudochama radians
Papyridea soleniformis

Only six eastward-dispersing species have broad ranges in the eastern Atlantic. *Cheilea equestris* (Calyptraeidae), the muricids *Thaisella coronata, Trachypollia nodulosa,* and *T. turricula,* and the bivalves *Nodipecten nodosus* (Pectinidae) and *Papyridea soleniformis* (Cardiidae) are widespread in West Africa as well as in the western Atlantic, and all have counterparts in the eastern Pacific.

Fossils referred to *Cheilea equestris* by Vokes (1975) from the early Miocene Chipola Formation of Florida indicate that this species has been in the western Atlantic for a very long time. It could have been derived from a species of the Eocene of Europe (Vokes, 1975). The genus *Cheilea* was present in Europe from Eocene to late Miocene (Tortonian) time, but the species *C. equestris* probably represents a secondary invasion of the eastern Atlantic from the west.

Species of *Thaisella* are known in the Americas since at least middle Miocene time. *T. coronata* is very similar or identical to *T. trinitatensis* (Guppy, 1869), which is known from the early Pliocene Cercado Formation of the Dominican Republic and still lives in the western Atlantic (Vokes, 1989). Typical *T. coronata* is also known from the western Atlantic, and has been in the eastern Atlantic since at least the Pleistocene (Rosso, 1974).

The scallop *Nodipecten nodosus* is widely if patchily distributed in the eastern Atlantic. In tropical America, *N. nodosus* can be traced back to the late Miocene (J. T. Smith, 1991), but in the eastern Atlantic the species has been reported as a fossil only from the late Pleistocene of the Canary Islands (Meco Cabrera, 1982).

The cardiid bivalve *Papyridea soleniformis* is widespread in the western Atlantic but has a very patchy distribution in the eastern Atlantic, where it is known from the Cape Verde Islands and Angola (Voskuil and Onverwagt, 1989). There is a closely related eastern Pacific species, *S. aspersa* (Sowerby, 1833).

Among westward-dispersing species (Table 2), only four (27% of 15 species) have or had very limited ranges in the western Atlantic. *Cymatium kobelti* has only been recognized in the western Atlantic as a fossil from the Pliocene of Colombia (Beu and Knudsen, 1987). The only western Atlantic occurrence of *C. trigonum* is off the coast of Venezuela (Finlay and Vink, 1982). Two other species, the bursids *Bursa marginata* and *B. scrobiculator,* are represented by Miocene to Recent populations in the eastern Atlantic, but have been reported in the western Atlantic only as late Pliocene or early Pleistocene fossils in the Móin Formation of Costa Rica (D. G. Robinson, pers. comm.).

Only one other purportedly amphi-Atlantic species has a markedly limited distribution in the western Atlantic.

Littoraria angulifera
Cerithium guinaicum
Hinea lineata
Charonia lampas
Cymatium kobelti
C. trigonum
Bursa marginata
B. scrobiculator
Ranella olearia
Epitonium albidum
Pugilina morio
Pseudomalaxis zanclaeus
Spirolaxis centrifuga
Mathilda barbadensis
Siphonaria pectinata

Vasum globulum Lamarck, 1816, is reported to occur in the Lesser Antilles as well as in West Africa (see Vokes, 1966, for a review). Faber (1988), however, has pointed out that the West African records of this species are erroneous, and that *V. globulum* is a western Atlantic species closely related to the southern Caribbean *V. capitellus* (Linnaeus, 1758).

Two other western Atlantic species with a very limited range are probably derived from eastern Atlantic species in relatively recent times. *Thais nodosa meretricula* Röding, 1798, known from islands off Brazil and from Ascension Island in the central south Atlantic, is distinct from but very closely related to the West African *T. n. nodosa* (Linnaeus, 1758) (see Rosewater, 1975; Leal, 1991). There is no similar species in tropical America, either living or fossil. The littorinids *Nodilittorina vermeiji* Bandel and Kadolsky, 1982, from islands off Brazil, and *N. miliaris* (Quoy and Gaimard, 1833) from Ascension Island, are extremely similar to the west African *N. granosa* (Philippi, 1848), but have no close relatives in the Americas (see Reid, 1989; Leal, 1991). As in the case of *Vasum globulus*, we have not included these two probable western Atlantic derivatives of eastern Atlantic taxa in our tally because of the absence of a fossil record.

The other westward-dispersing species are widely distributed in the western Atlantic, but most are unknown as fossils and therefore appear to be relatively recent immigrants to the American coasts. The melongenid *Pugilina morio*, which is found in mangrove environments from the southern Caribbean to Brazil, as well as in West Africa, is unknown as a western Atlantic fossil but is reported from the Pleistocene of West Africa (Rosso, 1974). Melongenids are abundantly represented as fossils in Miocene and Pliocene formations in the western Atlantic and eastern Pacific, but none of the species resembles *P. morio* and none can be referred to the genus *Pugilina.*

The pulmonate limpet *Siphonaria (Mouretus) pectinata* is not closely related to any other western Atlantic

siphonariid. Although the species has no fossil record, we interpret it as a westward disperser because it belongs to a subgenus that is otherwise known only from southern Africa and the northwestern Indian Ocean (see Hubendick, 1945, 1946). Morrison (1963) believed that *S. pectinata* was introduced by humans from West Africa, where it is abundant on rocky shores, to the western Atlantic. He pointed to the patchy distribution of the species in the Caribbean basin as evidence for this intepretation. Wave-exposed species such as *S. pectinata* are rarely susceptible to accidental human transport. Moreover, *S. pectinata* has a planktotrophic larva, which would under favorable circumstances make overwater dispersal possible. We therefore believe that *S. pectinata* dispersed from West Africa to the Americas in relatively recent times without the aid of people.

We have included the planaxid *Hinea lineata* among westward dispersers for two reasons. First, there is no fossil record of *Hinea* in tropical America, and no species of this genus occurs in the eastern Pacific (Houbrick, 1987, 1992). Second, although *Hinea* itself is not known as a fossil in the eastern Atlantic, there were middle Miocene species such as *Planaxis (Dalliella) dautzenbergi* Glibert, 1949, from the Helvetian (= Tortonian) of the Loire Basin in France, that have some features in common with *Hinea* (see Glibert, 1949). *H. lineata* is abundant and widespread on both sides of the tropical Atlantic.

Another likely recent immigrant from the east is the mangrove-associated littorinid *Littoraria (Littorinopsis) angulifera.* The subgenus *Littorinopsis* is diverse and widespread in the Indo-West-Pacific, and has existed in the eastern Atlantic since the early Eocene (Reid, 1986, 1989). It is unknown in the eastern Pacific, where the four extant mangrove periwinkles belong to the subgenera *Littoraria* s.s. and *Bulimilittorina* (see Reid, 1989). Woodring 1957) reported a small, almost completely decorticated, fossil from the early Miocene Culebra Formation of Panama as "*Littorina* sp. cf. *L. angulifera*". One of us (GJV) has examined this specimen at the U. S. National Museum of Natural History in Washington. The shell has a lower spire than do most species of *Littorinopsis*, but there are no preserved features that make distinction between *Littorinopsis* and *Littoraria s.s.* possible. The rich fossil record of the Pliocene of Florida contains several species of *Littoraria* (Petuch, 1991), but none is similar to *L. angulifera* and none belongs to the subgenus *Littorinopsis*. We therefore believe that *L. angulifera* arrived quite recently in the western Atlantic. We cannot exclude the possibility that *L. angulifera* is a late Pliocene or Pleistocene derivative of the Indo-West-Pacific *L. scabra* (Linnaeus, 1758), and that the Atlantic *L. angulifera* followed the dispersal route of other

immigrants from the Indo-West-Pacific. Under this scenario, *L. angulifera* would have originated in the western Atlantic and subsequently spread to the eastern Atlantic. This would imply that *Littorinopsis* had become locally extinct in West Africa before the arrival of *L. angulifera*. We know nothing about the Pliocene and Pleistocene fossil record of *Littorinopsis* in the Old World, but the mangrove biota of West Africa is quite rich in species and does not appear to have been ravaged by extinction. We therefore favor the hypothesis that *L. angulifera* dispersed westward to the Americas from Africa, and consider less likely the more complex hypothesis that the species invaded the western Atlantic from the Indo-West-Pacific and subsequently spread to West Africa.

Three other westward-dispersing species, *Ranella olearia* (Ranellidae), *Epitonium albidum* (Epitoniidae), and *Mathilda (Fimbriatella) barbadensis* (Mathildidae), all belong to lineages with a history extending to the early Miocene or Oligocene in Europe (see Glibert, 1949; Beu, 1976, 1980; Janssen, 1978a, b). To our knowledge, they have no American fossil record, and are not close to any eastern Pacific species.

Six of the 16 species inferred to have dispersed westward across the Atlantic are known as late Pliocene or Pleistocene fossils in the Americas. Three of these (*Cymatium kobelti*, *Bursa marginata,* and *B. scrobiculator*) are not known living in the western Atlantic today, and were discussed above. *Spirolaxis centrifuga* (Architectonicidae) has been reported from the late Pliocene or early Pleistocene Bowden Formation of Jamaica (Bieler, 1984), and *Cerithium guinaicum* appears in the correlative Moín Formation of Costa Rica (Houbrick, 1974). The ranellid *Charonia lampas* occurs in the early Pleistocene Mare Formation of Venezuela (Beu, 1976). None of these species has close relatives in the eastern Pacific, and none can be traced back beyond the late Pliocene in the western Atlantic. The lineages of *Bursa marinata, B. schrobiculator, Charonia lampas,* and *Spirolaxis centrifuga* extend back to the Miocene in Europe (see Beu, 1970, 1980; Bieler, 1984). The phylogenetic relationships of *Cerithium guinaicum* have not been worked out, but this species is the only member of its genus in America without either close eastern Pacific relatives or clear ancestors from the Miocene or early Pliocene (see Houbrick, 1974).

GENERAL DISCUSSION

From the analysis presented in the last two sections, we infer that at least 35 shallow-water shell-bearing molluscan species in the western Atlantic are late Pliocene or later invaders from the Indo-West-Pacific or eastern

TABLE 3. Summary of invasion of molluscs to and from the tropical Atlantic following uplift of the Central American isthmus.

Category	Number of Species
Invasion to western Atlantic	
Total	35
Invaders from Indo-West-Pacific	20
Invaders from eastern Atlantic	15
Narrowly distributed invaders	6
Invasion to eastern Atlantic	
Total	39
Invaders from Indo-West-Pacific	11
From western Atlantic	28
Narrowly distributed invaders	22

Atlantic, and that at least 39 species dispersed eastward across the Atlantic during this same time interval (Table 3). Eleven species derived from the Indo-West-Pacific are included in both tallies, because they probably first dispersed westward from the Indian Ocean to the Americas and subsequently spread eastward to the tropical eastern Atlantic. The number of westward dispersers would be increased by two if we included *Nodilittorina vermeiji* and *Thais nodosa meretricula*, which are probably western Atlantic derivatives of eastern Atlantic species.

Invaders comprise a small proportion of the faunas of the eastern and western Atlantic. Von Cosel (1982) estimated that the tropical eastern Atlantic molluscan fauna contains about 2220 species. The 39 post-isthmian invaders to that region therefore account for only about 2% of the fauna. No comparable estimates are available for molluscan diversity in the western Atlantic. However, Rosenberg (1993) reports that there are more than 2900 gastropod species between Cape Hatteras and Rio de Janeiro. The 35 shallow-water invaders to the western Atlantic therefore account for only 1.2% of this fauna. Locally, the contribution of invaders is higher, especially on oceanic islands. Thus, the molluscan fauna of the Cape Verde Islands comprises about 400 species (von Cosel, 1982), of which 27 (6.8%) are invaders from the west by our count. Of the 121 prosobranch gastropod species at Fernando de Noronha off Brazil (Leal, 1991), seven (5.8%) are identified by us as invaders from the Indo-West-Pacific or eastern Atlantic. This tally does not include *Nodilittorina vermeiji* or *Thais nodosa meretricula*, both of which appear to be derived from eastern Atlantic taxa.

Most of the dispersal across the Atlantic and from the Indo-West-Pacific is probably by planktonic larvae. Scheltema (1971) has documented the existence of planktonic larvae of many amphi-Atlantic species in the open ocean far from land, and has provided evidence that larvae remain competent to settle for many weeks or even months. It is possible, however, that several mangrove-associated

species dispersed by rafting as adults on wood. *Littoraria angulifera, Thaisella coronata,* and *Pugilina morio* are typical of mangrove environments, and all can be found on logs as well as on living trees.

Whether dispersal is by planktonic larvae or by rafting adults, the routes of dispersal reflect the pattern of oceanic circulation in the Atlantic. In the southern Atlantic, the strongest trans-oceanic currents flow westward (Leal, 1991), whereas in the North Atlantic the strong Gulf Stream flows eastward (see also Scheltema, 1971). The fact that several invaders to the western Atlantic from the Indo-West-Pacific and eastern Atlantic are known mainly from South and Central America suggests to us that westward dispersal of these species was largely across the south Atlantic. Similarly, many eastward-dispersing species are restricted in the eastern Atlantic to the Cape Verde Islands, Canary Islands, or Mediterranean area. This, we believe, implies that eastward dispersal is chiefly a North Atlantic phenomenon.

Ocean currents provide the means for dispersal, but they are not alone in determining the pattern of invasion of species. Propagules can be brought to a potential recipient region, but if they fail to settle, thrive, and reproduce, the invasion is ephemeral. Conditions in the recipient biota must therefore be understood if we are to explain observed patterns of interchange among biotas.

The available evidence indicates that the tropical western Atlantic received approximately the same number of shallow-water immigrants (35 species) as this region exported to the eastern Atlantic (28 species). The eastern Atlantic received more species (39) than it exported (16). However, the majority of invaders to the eastern Atlantic (28 of 39 species, 72%) have extremely limited distributions in the eastern Atlantic, where they are confined either to offshore islands or to small sectors of the mainland coast. By contrast, most of the immigrants to the western Atlantic have wide ranges there; only four of the 35 species (11%) can be described as narrowly distributed in the western Atlantic. These data imply that penetration of the eastern Atlantic by immigrants has been marginal, whereas invasion of the western Atlantic has been geographically much more extensive.

The status of the eastern and western Atlantic as donor and recipient regions for invaders can be compared with that of other tropical marine regions. Since the Central American seaway closed during the middle Pliocene, the eastern Pacific has received a large number of immigrant species from the Indo-West-Pacific, especially in reef habitats (Vermeij, 1987, 1991b; Grigg and Hey, 1992). Emerson (1991) recorded 61 shell-bearing gastropods as invaders from the Indo-West-Pacific to the eastern Pacific. To our knowledge, the eastern Pacific has not exported species to

other tropical regions since mid-Pliocene time. Although many of the Indo-West-Pacific immigrants are found only on offshore islands, at least 26 (46%) have penetrated to the Pacific mainland coast of the Americas. The Indo-West-Pacific has served as a donor region for many invaders to the eastern Pacific and Atlantic. We know of only one persuasive case of recent immigration to the Indo-West-Pacific from elsewhere. Lozouet (1986) has marshalled strong arguments in favor of the hypothesis that the lagoonal potamidid gastropod *Potamides conicus* Blainville, 1828, invaded the Indian Ocean from the Mediterranean during late Pliocene or Pleistocene time. It is, of course, possible that other taxa have a similar history, but detailed documentation is lacking.

The four tropical marine regions can thus be ranked according to their status as donor and recipient regions for recent molluscan immigrants. The Indo-West-Pacific has been chiefly a donor region, whereas the eastern Pacific has been only a recipient region. The eastern and western Atlantic regions fall in the middle.

These patterns of invasion could reflect the extent of prior extinction of species in the various tropical regions (Vermeij, 1991b). Among the four biotas, that of the Indo-West-Pacific probably suffered the smallest loss in overall diversity during the Pliocene and Pleistocene. Only a few taxa at the generic level disappeared from the region, although many genera and species apparently underwent contractions in range during the last three million years (Vermeij, 1986, 1991c). The western Atlantic, on the other hand, has been greatly affected by extinction. Some 60 to 70% of species and 32% of subgenera became extinct in Florida after mid-Pliocene time. Although all of this loss was compensated for, mainly by speciation, the Pliocene represents a time of very high species turnover in Florida and in other parts of the western Atlantic (see Vermeij and Petuch, 1986; Allmon *et al.*, 1993). Extinction in the eastern Pacific at the generic level was less than half that in the western Atlantic; at the species level, there was also substantial extinction, but most of the losses were compensated for by extensive speciation during the early Pleistocene, so that there may have been no net loss in diversity since the early Pliocene. No published estimates of extinction exist for the tropical eastern Atlantic, because no substantial Pliocene deposits are known from West Africa. Brébion (1979) summarized the Pliocene and Pleistocene molluscs of Morocco (now in subtropical West Africa). From his list we estimate that 21 of 87 species (24%) recorded from the Pliocene and early Pleistocene of Morocco are extinct. There are only two genera that no longer occur in the eastern Atlantic. This calculation suggests that extinction in this part of the world was much less severe than in the

western Atlantic. Tropical West Africa and the tropical eastern Pacific have both been recognized as major refuges for taxa that disappeared from southwestern Europe and the western Atlantic during the Pliocene and early Pleistocene (Vermeij, 1986, 1991c).

The western Atlantic thus stands out as the region that has suffered the greatest loss of diversity during the Pliocene and Pleistocene. Although the known number of invaders in this region is small, most of the invading species have achieved wide distributions in the western Atlantic and have become common elements in the habitats they occupy. The eastern Atlantic has received a large number of immigrant species, but few have become geographically widespread and very few have become common in shallow waters. Indeed, it is not at all certain that many of the immigrant species maintain self-perpetuating populations in the eastern Atlantic. The same situation applies to the eastern Pacific. Many species have immigrated to this region, but very few have become common, and many eastern Pacific populations of Indo-West-Pacific species may be sustained only by the periodic influx of dispersing larvae from the west (see also Richmond, 1990; Emerson, 1991; Grigg and Hey, 1992). Immigration to the Indo-West-Pacific has been negligible and ecologically marginal. Thus, the greatest penetration of immigrants has occurred in the region that suffered the greatest magnitude of extinction and the greatest net loss of diversity since the Pliocene. Biotas in which the loss of diversity has been lower have been less extensively infiltrated by species invading during late Pliocene or Pleistocene time. Similar patterns have been documented for other cases of marine as well as terrestrial interchange (Vermeij, 1991a, b).

There is some evidence that patterns of invasion before the middle Pliocene were different from those later. In particular, eastward dispersal in the Atlantic may be a relatively recent phenomenon. Although systematically collected data for trans-Atlantic faunal interchange are not available for the Miocene, detailed studies of pectinid bivalves (Waller, 1991) and muricid gastropods (Vokes, 1988) indicate that many Miocene and early Pliocene taxa in tropical America owe their origins to immigration from the east. Examples include the pectinid scallop lineages of *Aequipecten mucosus* (Wood, 1828) and *Argopecten*, and the muricid lineages *"Hexaplex" brassica* (Lamarck, 1822) and *Muricanthus*. Much stronger ties link the faunas of the eastern Atlantic and tropical America during the Eocene. Dozens of genera and species occurred on both sides of the Atlantic, and may have dispersed from east to west (see e.g. Squires, 1987; Givens, 1989, 1991; Allmon, 1990). We know of no documented cases of eastward dispersal until middle Pliocene time. In the tropical Pacific, westward dispersal may also have been the rule during the early

Cenozoic (Grigg and Hey, 1992). These patterns of dispersal probably reflect the predominantly westward flow of ocean currents at a time when a more or less continuous belt of tropical seaway existed at low latitudes before seaways through the Middle East, Indonesia, and Central America were constricted. Eastward dispersal in the Atlantic may have become possible when circulation in the North Atlantic (especially that in the Gulf Stream) became more vigorous during the middle Pliocene (Kaneps, 1979; Maier-Reimer *et al.*, 1990; Crowley, 1991; Crowley and North, 1991). Whether prior loss of diversity also played a role in the pattern of interchange during Miocene and earlier Cenozoic time is unknown. Our knowledge of the taxonomy and distribution of Miocene and older species is still too sketchy to permit firm conclusions to be drawn. We hope that studies of Cenozoic molluscs on a worldwide scale will be done, so that important questions about faunal interchange and extinction can be answered.

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APPENDIX 1.

List of western Atlantic species likely to have arrived from the Indo-West-Pacific region after closure of the Central American isthmus. An asterisk indicates that the species is endemic to the Atlantic but very closely related to an Indo-West-Pacific taxon; other species occur in both Atlantic and Indo-West-Pacific regions.

Gastropoda:
* *Synaptocochlea picta* (Orbigny, 1842)
* *Casmaria atlantica* Clench, 1944
* *Malea (Quimalea) noronhensis* Kempf and Matthews, 1969
  Tonna galea (Linnaeus, 1758)
* *T. maculosa* (Dillwyn, 1817)
  Eudolium bairdii (Verrill and Smith, 1881)
* *E. crosseanum* (Monterosato, 1869)
* *Bufonaria (Marsupina) bufo* (Bruguière, 1792)
* *Bursa (Bufonariella) natalensis* (Coelho and Matthews, 1970)
  B. (Bufonariella) ranelloides (Reeve, 1844)
* *B. (Lampadopsis) thomae* (Orbigny, 1842)
  Distorsio perdistorta Fulton, 1938
  Cymatium (Turritriton) comptum (A. Adams, 1855)
  C. (Ranularia) gallinago (Reeve, 1844)
* *C. (Septa) occidentalis* Clench and Turner, 1957
  C. (Reticutriton) pfeifferianum (Reeve, 1844)
* *C. (Ranularia) ridleyi* (E. A. Smith, 1890)
  C. (Turritriton) vespaceum (Lamarck, 1822)
  Gyrineum louisae Lewis, 1974
* *Psilaxis krebsii* (Mörch, 1874)

APPENDIX 2.

List of shallow-water amphi-Atlantic shell-bearing molluscan species. Species occur at depths of 100 m or shallower. An asterisk indicates that there is no close eastern Pacific relative or that the fossil record of the species or its presumed ancestor does not precede the late Pliocene in the western Atlantic. Species without further annotations are known to be living on the continental coasts of both the eastern and western Atlantic. Those living in the eastern Atlantic only on offshore islands (Canary Islands, Cape Verde Islands, or Madeira) are designated "insular EA". Species known in the western Atlantic only from offshore islands are designated "insular WA". Species known in the western Atlantic only as fossils are designated "fossil WA".

Gastropoda:
  Scissurella cingulata (O. G. Costa, 1861)
  Diodora cayenensis (Lamarck, 1822) (insular EA)
  E. tuberculosa (Libassi, 1859)
  Lucapinella limatula (Reeve, 1850)
* *Littoraria (Littorinopsis) angulifera* (Lamarck, 1822)
  Nodilittorina (Fossarilittorina) meleagris (Potiez and Michaud, 1838)
* *Benthonella gaza* Dall, 1889
  Alaba incerta (Orbigny, 1842)
  Cerithium (Thericium) atratum (Born, 1778)
* *C. (T.) guinaicum* Philippi, 1849
  Fossarus ambiguus (Linnaeus, 1767)
* *Hinea lineata* (da Costa, 1778)
  Crepidula (Bostrycapulus) aculeata (Gmelin, 1791) (insular EA)
  Cheilea equestris (Linnaeus, 1758)
  Hipponix antiquatus (Linnaeus, 1767) (insular EA)
  H. subrufus (Lamarck, 1819) (insular EA)
  Pedicularia sicula (Swainson, 1840)
  Trivia (Dolichupis) candidula (Gaskoin, 1836)
  Lamellaria perspicua (Linnaeus, 1758)
* *Gyrodes depressa* (Seguenza, 1874)
* *Natica livida* (Pfeiffer, 1840) (insular EA)
  Notocochlis marochiensis (Gmelin, 1791)
  Polinices lacteus (Guilding, 1834) (insular EA)
  Cassis tuberosa (Linnaeus, 1758) (insular EA)
  Cypraecassis testiculus (Linnaeus, 1758)
  Phalium (Tylocassis) granulatum (Born, 1778) (insular EA)
  Bursa (Lampadopsis) corrugata (Perry, 1811) (insular EA)
* *B. (Apsa) marginata* (Gmelin, 1791) (fossil WA)
* *B. ranelloides* (Reeve, 1844) (insular EA)
  B. (Bufonariella) granularis (Röding, 1798) (insular EA)
* *B. (Bufonariella) scrobiculator* (Linnaeus, 1758) (fossil WA)
* *B. (Lampadopsis) thomae* (Orbigny, 1842) (insular EA)
* *Distorsio perdistorta* Fulton, 1938
  Charonia tritonis variegata (Lamarck, 1816)
* *C. lampas* (Linnaeus, 1758)
  Cymatium (Monoplex) aquatile (Reeve, 1844) (insular EA)
* *C. (Turritriton) comptum* (A. Adams, 1855)
  C. (Ranularia) cynocephalum (Lamarck, 1816)
  C. (Turritriton) kobelti (von Maltzan, 1884) (fossil WA)
  C. (T.) labiosum (Wood, 1828) (insular EA)
  C. (Monoplex) martinianum (Orbigny, 1845)
  C. (Ranularia) muricinum (Röding, 1798) (insular EA)
  C. (Monoplex) nicobaricum (Röding, 1798)
* *C. (Septa) occidentale* Clench and Turner, 1957 (insular EA)
  C. (Monoplex) parthenopeum (von Salis, 1793)
  C. (Turritriton) tenuiliratum (Lischke, 1863)
* *C. (Monoplex) trigonum* (Gmelin, 1791)
* *Gyrineum louisae* Lewis, 1974
  Linatella caudata (Gmelin, 1791) (insular EA)
  L. succincta (Linnaeus, 1771)
* *Ranella olearia* (Linnaeus, 1758)
* *Eudolium bairdii* (Verrill and Smith, 1881)
* *E. crosseanum* (Monterosato, 1869)

* *Tonna galea* (Linnaeus, 1758)
* *T. maculosa* Dillwyn, 1817 (insular EA)
* *Cosmotriphora melanura* (C. B. Adams, 1850)
  Metaxia abruptu (Watson, 1880)
  Oceanida graduata (de Folin, 1870)
  Cylindriscala acus (Watson, 1883)
* *Epitonium (Hyaloscala) albidum* (Orbigny, 1842)
  E. (Gyroscala) lamellosum (Lamarck, 1822)
  E. striatissimum   (Monterosato, 1878)
  Opalia (Dentiscala) crenata (Linnaeus, 1758)
  Scalenostoma subulatum (Broderip, 1832)
  Cytharmorula grayi (Dall, 1889)
  Stramonita haemastoma (Linnaeus, 1767)
  Thaisella coronata (Lamarck, 1822)
  Trachypollia nodulosa (C. B. Adams, 1845)
  T. turricula (von Maltzan, 1884)
* *Typhis (Typhina) belcheri* Broderip, 1833
* *T. (Typhinellus) sowerbii* Broderip, 1833
  Coralliophila caribaea Abbott, 1958 (insular EA)
  C. squamosa (Bivona, 1838)
  Colubraria testacea (Mörch, 1852) (insular EA)
* *Pugilina morio* (Linnaeus, 1758)
  Mitrella ocellata (Gmelin, 1791)
* *Vasum globulus* Lamarck, 1816 (insular WA)
  Gibberula lavalleeana (Orbigny, 1842)
  Persicula interruptolineata (von Mühlfeld, 1816)
  Prunum marginatum (Born, 1778)
  Conus (Chelyconus) ermineus (Born, 1778)
* *Corinnaeturris leucomata* (Dall, 1881)
  Drilliola loprestiana (Calcara, 1841)
  Gymnobela agassizii (Verrill and Smith, 1880)
  Architectonica nobilis (Röding, 1798)
  Discotectonica discus (Philippi, 1844)
  Heliacus bisulcatus (Orbigny, 1842)
  H. cylindricus (Gmelin, 1791)
  H. perrieri (Rochbrune, 1881)
  Pseudotorinia architae (O. G. Costa, 1841)
* *Psilaxis krebsii* (Mörch, 1874)
* *Spirolaxis centrifuga* (Monterosato, 1890)
* *Mathilda (Fimbriatella) barbadensis* (Dall, 1889)
  Eulimella scillae (Scacchi, 1835)
  Pyramidella dolabrata (Linnaeus, 1758)
  Hydatina physis (Linnaeus, 1758)
  Micromelo undatus (Bruguière, 1792)
  Philine trachyostraca (Watson, 1897)
  Cylichna discus Watson, 1883
  Bulla striata (Bruguière, 1792)
  Atys caribaeus (Orbigny, 1842)
  A. macandrewi E. A. Smith, 1872
  Haminoea antillarum (Orbigny, 1841)
  H. elegans (Gray, 1825)
  Umbraculum umbraculum (Lightfoot, 1786)
  Berthella stellata (Risso, 1826)
  Pira monilis (Bruguière, 1792)
* *Siphonaria (Mouretus) pectinata* (Linnaeus, 1758)

Scaphopoda
  Dentalium striolatum Stimpson, 1851

Bivalvia
  Arca imbricata Bruguière, 1789 (insular EA)
  Arcopsis adamsi (Dall, 1886) (insular EA)
  Pinna rudis (Linnaeus, 1758)
  Lima lima (Linnaeus, 1758)
  Perna perna (Linnaeus, 1758)
  Lithophaga aristata (Dillwyn, 1817)
  Nodipecten nodosus (Linnaeus, 1758)
  Dendostrea frons (Linnaeus, 1758) (insular EA)
* *Neopycnodonte cochlear* (Poli, 1795)
* *Parahyotissa mcgintyi* Harry, 1895
  Pseudochama radians (Lamarck, 1819) (insular EA)
  Papyridea soleniformis (Bruguière, 1792)
  Gastrochaena hians (Gmelin, 1791)
  Barnea truncata (Say, 1822)
  Pholas (Thovana) campechiensis (Gmelin, 1791)